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Growth, larval development and metamorphosis in small-mouthed salamanders (Ambystoma texanum)

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Abstract

The small-mouthed salamander (*Ambystoma texanum*), a common species in the midwestern United States, lays its eggs in temporary ponds during mid to late March once they have filled with water from the melting winter snow or early spring rains. For its relative abundance in the Midwest, there is little known about the life history of this species. My research followed the growth of small-mouthed salamander larvae in ponds between hatching, which occurred in early spring (mid-April), and metamorphosis, which occurred in midsummer (early June to mid-July). The research focused on the growth, larval development, and timing of metamorphosis with special attention paid to the age and body size at metamorphic climax. I found a minimum period of about 2 months for metamorphosis completion for rapidly progressing individuals, with the full cohort finishing transformation by 3-3.5 months. Further research and descriptive studies like this one will be needed to better understand the ecology of this species for the purpose of its long term conservation.

Introduction

Amphibians show remarkable diversity of life histories and they are similarly diverse in their reproductive modes. These approaches range from oviparity to viviparity and from aquatic to terrestrial reproductive modes (Duellman and Trueb 1986). Despite this variation, the majority of amphibians have complex life histories with an aquatic larval stage and a terrestrial adult stage. Larvae are often characterized as being aquatic, remaining in a small area, and having a primary purpose of growth and development, where as adults are mobile and terrestrial with a primary objective of reproduction and

dispersal (Werner 1986, Wilbur 1980). Growth may still be an important issue in the adult stage but its significance tends to vary considerably among lineages (Werner 1986, Wilbur 1980).

Depending on the surrounding environment, amphibian larvae can metamorphose at an early age or they can opt to remain in the larval stage for a longer period of time to maximize growth (Wilbur and Collins 1973). This variation in developmental period is a type of phenotypic plasticity, which is the ability of an organism to change its phenotype in response to changes in the environment. The timing of metamorphosis is just one of several traits that exhibit phenotypic plasticity in amphibians. For instance, some species can change their rate of development and may even opt out of metamorphosis if the aquatic environment is favorable and stable (Altwegg 2002, Laurila *et al.* 2002). Opting out of metamorphosis and becoming a mature adult while remaining in the same environment and body configuration as the larval stage is known as paedomorphism and has evolved independently in many urodele (salamander) families, including ambystomatids (Eagleson 1976, Rose and Armentrout 1976, Sexton and Bizer 1978). Some other traits that show phenotypic plasticity in amphibians include growth rate and size at metamorphosis (Collins 1979, Patranka and Sih 1986, Smith 1987, Stenhouse 1985, Wilbur 1980, Wilbur and Collins 1973). In environments that are highly variable, selection for phenotypic plasticity is more effective then selection for genetic variation (Caswell 1983, Kaplan and Cooper 1984, Via and Lande 1985). Selection for plasticity leads to greater flexibility to react to variable or rapidly changing environmental conditions. There are other ways to deal with environmental stochasticity including shortening the larval period itself. This can be done by either selecting for faster

developmental rates or by selecting for increased competitive ability and foraging rate to increase rate of development via plastic responses to food availability (Wilbur and Collins 1973).

In urodeles, direct development, progression directly from the zygote to the adult without a larval stage, and paedomorphosis, either obligate as in the cases of *Nectrus maculosus* and *Ambystoma mexicanum* or facultative as in the cases of *A. tigrinum* and *A. gracile*, are the most common life histories (Werner 1986). Direct development is seen in the plethodontid salamanders, the most speciose group of urodeles, though some other families have only paedomorphic species. In some newts, double metamorphosis occurs where the aquatic larva will metamorphose into a terrestrial eft stage before eventually metamorphosing yet again into an aquatic adult stage. This wide range of variation in life cycles within amphibians gives these species considerable latitude for selection by local environments for certain life history characteristics (Werner 1986).

Since most amphibians depend on aquatic environments for egg deposition and the larval stage of development, amphibian life histories place a great deal of importance on wetland habitats. There are two general types of wetlands: permanent and ephemeral. Permanent wetlands remain filled with some level of water throughout the entire year. Ephemeral ponds are seasonal, often filling in late winter to early spring and drying out by late summer to early fall. Both types of wetlands offer different advantages and disadvantages to their resident amphibian populations. In permanent ponds and wetlands, larvae are free to stay in the aquatic environment until they reach their maximum size (Werner 1986) and have a greatly reduced risk of desiccation (Licht and Bogart 1990, Spright 1968). Most species that breed in permanent ponds have a reduced time to sexual

maturity and females may have increased fecundity (Semlitsch 1987b, Semlitsch *et al.* 1988). Ephemeral ponds and wetlands on the other hand, balance a trade-off between an environment free of predatory fish and an increased risk of desiccation (Phillips *et al.* 2002). Ephemeral ponds are also known as hotspots for high primary productivity, with fewer potential predators for amphibian larvae (Heyer *et al.* 1975, Woodward 1983). Werner (1986) made comparisons and examined metamorphosis among amphibian orders. He found that size at metamorphosis versus adult size is constrained phylogenetically but also shows variation within families. Werner's model predicts how the balance of size specific growth will first favor one habitat and then another. By these models, forecasts can be made for the life histories of different amphibian families. If growth rates are rapid in the aquatic environment, then metamorphosis may be delayed to maximize time in a high growth environment. If growth is slow, then metamorphosis can be triggered at an earlier time.

There are several conditions that are considered "unfavorable" for amphibians and have been shown to have detrimental effects on their populations. Some of these include high predation and habitat drying risks. These factors often lead to a decreased larval period and a decreased size at metamorphosis in an attempt to decrease the cumulative risk to the larvae by leaving the aquatic environment as soon as possible (Berven 1982, 1990, Berven and Gill 1983, Pough and Kamel 1984, Smith 1987). Also, if resources are limited in the environment, larvae can slow metamorphosis to reach a larger or at least a minimum body size (Semlitsch and Caldwell 1982, Travis 1984). "Favorable" conditions such as low predation risk and low risk of desiccation lead to longer larval periods and increased body sizes at metamorphosis (Berven 1982, 1990, Berven and Gill 1983).

Werner (1986) found that predation risk decreased with increasing body size. Increased size in males also enhances mating success where as in females it increases fecundity, while generally increasing the probability of overwinter survival and decreasing time to first reproduction (Berven 1982, 1990, Berven and Gill 1983, Pough and Kamel 1984, Smith 1987). In environments where resources are nearly unlimited, individuals metamorphose at similar body sizes and have comparable larval period lengths (Semlitsch and Caldwell 1982, Travis 1984).

Since ephemeral ponds represent an environment that is relatively free from predation, it makes them an ideal habitat for amphibian larvae. It also means that hydroperiod, the period of time during which the wetland is inundated with water, is of critical importance to the developing larvae (Semlitsch *et al.* 1996). Studies have shown that early drying years have resulted in mass mortality rates among larval amphibian populations (Calef 1973, Ryan and Bruce 2000). The timing of filling can also have a major effect on the dynamic of the pond environment as it can effect interspecific competition and predator-prey relationships (Boone *et al.* 2002, Rowe and Dunson 1995). Often times reduced hydroperiods lead to faster growing individuals metamorphosing earlier and closer to optimal size, while slower growing individuals metamorphose later and closer to minimum size (Phillips *et al.* 2002). When hydroperiod is extended, all individuals metamorphose at optimal size and there is no relationship between size at and time of metamorphosis (Phillips *et al.* 2002). Ambystomatid larvae have been known to slow down their rate of metamorphosis if hydroperiods are extended, especially if conditions in the pond are good as well (Rowe and Dunson 1995). For these reasons, the major factors contributing to the stability of complex life histories in amphibians include

the adaptive significance of their ability to exploit temporary pond opportunities while weighing them against predation and desiccation risks (Wassersug and Seibert 1975, Wilbur and Collins 1873, Wilbur 1980, 1984). It should also be noted that there is a difference between ephemerality and variability. A stable, ephemeral wetland gradually dries over the course of the season at a near constant rate and has a fairly predictable hydroperiod. A variable, ephemeral wetland will similarly dry over the course of the season, but the overall drying rate could vary greatly during this time, with the wetland quickly draining and refilling due to warm temperatures and inconsistent, but heavy rains, respectively. Hydroperiod may also vary on a year to year basis. This difference leads to differing degrees of phenotypic plasticities among populations who experience stable ephemeral wetland environments and those who experience variable ephemerality in wetland environments. This difference leads to a greater magnitude of phenotypic plasticity in the more variable ephemeral habitats than in their stable counterparts (Lieps *et al.* 2000).

Timing of metamorphosis can have a major impact on many factors in an amphibian's life history. It influences body size at metamorphosis which has an impact on an individual's survival, body size at first reproduction, age at first reproduction, and fecundity (Semlitsch *et al.* 1988, Smith 1987). Time of and size at metamorphosis can both be affected by crowding, lack of food, quality of diet, and temperature (Collins 1979, Pandian and Marian 1985, Smith-Gill and Berven 1979, Wilbur 1976). Intra- and interspecific densities, aquatic predator density, food availability, temperature variation, swimming volume, oxygen availability, dissolved carbonic acid, conductivity, and external hormonal or hormonal metabolite concentrations have also been shown to

influence the time of and size at metamorphosis (Denver 1997a, 1997b, Denver *et al.* 1998, Newman 1987, 1989, 1994, Semlitsch 1987a, Skelly 1996, Tejedo and Reques 1994, Wilbur 1987). The optimal timing of metamorphosis requires compromises between growth, development, and survival of the larva with the growth, reproduction, and survival of the adult (Istock 1967, Stearn and Koella 1986, Werner 1986, Wilbur 1986). Longer larval periods are usually indicative of harsh adult environments where food is scarce, weather is severe and unreliable, or sufficient cover is lacking. Shorter larval periods stem from individuals trying to exploit environments that deteriorate seasonally where predation increases, food becomes scarce, and the habitat may dry out as the season progresses (Wilbur and Collins 1973, Bruce 1979, Spurles 1974, Slade and Wassersug 1975, Wilbur 1980).

With increasing urbanization it has become progressively more common to see permanent and ephemeral wetlands, the primary breeding grounds for amphibians, drained for development. The loss of permanent and ephemeral wetlands has caused a drastic drop in species abundance and diversity of many amphibian families across the world. To help combat this rising issue, state and national governments have issued statutes that help to protect wetlands as centers for species diversity. Some of these laws pertinent to the study area include the Clean Water Act (Section 404), Indiana Code 13-18-22 – State Regulated Wetlands, and Indiana Water Quality Standards. Though these laws help protect the loss of wetlands, and may require the restoration of other wetland areas when a developer drains a new one for development, they sometimes fall short of restoring the complexity of the wetlands that are being reestablished. A majority of these manmade wetlands are permanent and therefore cannot support the species that are

dependent on ephemeral wetlands. Many species do not fare well in manmade wetlands, which are usually stocked with predatory fish, because they lack the anti-predator behavior necessary to survive in such habitats since they are used to predator free ephemeral wetlands (Sih *et al.* 2000).

Even though positive strides are being made, amphibian populations are decreasing in number across the globe (Plough *et al.* 2009), mainly due to habitat loss, development of wetlands, etc. It is therefore imperative that we understand how these organisms live if we are to help amphibian populations recover. Often times, new wetlands created to replace those lost due to land development, lack locations where temporary ponds can form, thereby providing no location for amphibians to successfully breed and establish populations. Understanding life histories will be critical in providing relevant data so that a better plan for conservation can be put into effect.

Life History and Range of Ambystoma texanum

Ambystoma texanum is common throughout the south-central United States, with the exception of the Ozark Plateau and the Louisiana Gulf Plain. The range of *A. texanum* extends from eastern Texas and Oklahoma to southeast Nebraska up to southeast Michigan, northern Ohio, and eastern Kentucky and Tennessee, and down to western Alabama (Figure 1). Researchers believe that this current range constitutes the species' historic range as well (Trauth, 2005). *Ambystoma texanum* are considered abundant throughout their range with the exception of Michigan where they are considered an endangered and protected species. Populations throughout its range have been eliminated

as flood plain and mesic forests are clear cut and transformed into agricultural fields (Trauth, 2005).

Adults inhabit underground burrows for the majority of the year but can occasionally be found on the surface under debris such as logs and leaf litter. Adults normally remain within a 75 m radius of the pond where they hatched, and return to the same area for breeding, though migration is possible if there are other breeding sites within reach of the individual's birth site. Adults migrate from upland sites to breeding wetlands in late winter and early spring. This movement is often cued by the regular warm rains that often fall during that time of year, though they will make the migration even without this environmental cue. The timing of the breeding migration differs among latitudes within the species' range, due to seasonal temperature differences. Breeding and egg laying occur respectively around and in seasonal to semi-permanent wetlands including: prairie potholes, forested wetlands, oxbows, ditches, borrow pits, flooded fields, and occasionally stream pools (Trauth, 2005).

Male *A. texanum* leave spermatophores which the females select to fertilize their eggs. Females may lay clumps of 1-15 eggs on submerged branches in the pond or simply along the substrate of the wetland floor. They can deposit between 550 and 700 eggs per season. Incubation lasts between 2-8 weeks depending on the temperature of the pond water. Once hatched, larvae develop and finish metamorphosis during early to midsummer. The larvae are gape limited feeders and may be cannibalistic. Common predators include aquatic insects, larval insects, garter snakes (*Thamnophis* sp.), and water snakes (*Nerodia* sp.) (Trauth, 2005).

I conducted a descriptive study of the larval life history of small-mouthed salamanders. *Ambystoma texanum* breeds in temporary ponds in late winter with hatching occurring in early spring, and metamorphosis, occurring in midsummer. My research focused on the timing of metamorphosis with special attention to the age and body size at metamorphic climax. There have been few field studies done in regards to the life history of *A. texanum*, with anecdotal data suggesting time to metamorphosis at 2-4 months, though it could vary based on the hydroperiod (Minton 2001, Petranka 1998, Phillips *et al.* 2002). An experimental study by Ryan (2007) showed that the minimum time needed to complete metamorphosis was approximately 2 months. This study was undertaken using populations of larvae in artificial "ponds" with three treatment groups of varying hydroperiod: 50 days, 75 d, 100 d, and constant (control). Therefore, the goal of this study was to examine and describe how the life history of *Ambystoma texanum* plays out in its natural environment.

Materials and Methods

Study Area

The study was carried out in Eagle Creek Park, with lab work being conducted at Butler University, in Indianapolis, Indiana. Suitable breeding wetlands were surveyed for *A. texanum* egg clutches in late March of 2009 by inspecting the pond floor and checking submerged sticks and limbs for the presence of egg clutches. Four sites were selected for the study that had abundant eggs and/or larvae. These sites were selected not only based on the presence of potential larvae, but also because of the differences between their surrounding microhabitats.

The first site was a man made ditch approximately 1.6 m by 6 m, with a maximum filling depth of 66 cm. This site, hereafter called "the Hole," is in the middle of a large open field with scattered shrubs and thickets. One such shrub grew on the west side of the ditch and provided it with shade for the first half of the day. The floor and walls of the Hole were composed of sand and mud. The second site, Kirtland's Pond, is a semi-permanent pond with an approximate area of 2,500 m^2, with a maximum depth of about 1 m. Kirtland's Pond is surrounded by a similar field and shrub habitat, with woodland lying further to the north and east. Kirtland's Pond had a thick mud bottom and with many reeds and cattails (*Typha* sp.) in the pond itself.

The third and forth sites were natural, forested wetlands. Site three, "I-465 Pond," was located in the forest interior adjacent to an open field with scattered shrubs. The site at maximum filling covers approximately the same area as Kirtland's Pond, with a maximum depth of 45 cm. The forth site, "the Maintenance Pond," was again located in the forest interior and was adjacent to a small paved utilities road. The site at maximum filling had an approximate area of 1250 m^2, with a maximum depth of 50 cm. The substrate of the pond floor for both sites consisted primarily of leaf litter.

Capture and Transport

Collection of larvae began once eggs hatched at a given site and occurred weekly from April 14, 2009 till July 14, 2009 when the last site had dried and no more larvae were present at the site. The ponds were sampled using a dip net to capture individuals; the net was shuffled along the pond floor as to scare up any larvae hidden under the leaf litter. Individuals were also captured from the water column itself and by shuffling the

net along the sides of the ponds, where some individuals hid in the overhanging vegetation. For each sampling bout, 20-30 individuals were taken from each pond. If no individuals were observed after 20 minutes of searching, it was assumed that there were no individuals left at the site.

Initially, captured individuals from one site were kept in a single 400 mL plastic container until they were transported back to the lab and deposited into a 1.5 L plastic tub. Later in the study when individuals began to vary greatly in size and level of development, larvae were held in groups of similarly sized individuals or were isolated in individual 100 mL plastic containers for the duration of the transport to and from the lab as well as in the lab itself. This was done to reduce the likelihood of cannibalistic events that would have been facilitated by the capture and transport process.

Presence of other animals within the pond was also noted during the weekly collections as well as the relative abundance of the larvae, the state of the wetland (drying or not), presence of algae, etc.

Measurements

Once at the lab, the mass of the individuals was taken using a top loading electronic balance. The individuals were sucked up from their holding containers using a plastic pipette and were then lightly blotted with a paper towel before being added to a cup of water resting on a zeroed balance. The mass was recorded to the nearest 0.001 g for each individual.

The developmental stage was then determined visually using a Leica S4E dissecting microscope. The characteristics for the basis of the staging and the

developmental stages themselves were adapted from the methods of Donavan (1980) with slight alterations. When individuals were found to be ambiguous between two of the stages, they were given the average of the two (i.e., if the individual was between 45 and 46 then it was assigned 45.5). Stage 52 of Donavan's model was also broken into two distinct groups – 52 and 52.5 with the intermediate groups of 52/52.5 → 52.25 and 52.2/53 → 52.75. Once the individuals had reached a safe size for handling, approximately 0.5 g, their snout-vent length (SVL), the length from the tip of the salamander's nose to the anterior end of the cloaca, was also recorded using a clear, plastic ruler.

After all measurements had been taken, all individuals were returned to their respective ponds.

Analysis

Hatching time was inferred based on growth and the interval between when the site was surveyed with no individuals present and when individuals were first observed at the site. The minimal period necessary to reach metamorphosis was calculated by subtracting the day of the first observed metamorphic individual from the inferred date of hatching for the site. A ratio of metamorphic individuals per sample was calculated and the average daily growth rate were determined by subtracting the average mass of the current week from that of the previous week, then dividing that value by the number of days between sample collections. A one-sample t-test was done to compare the average size of metamorphs from the Hole to that of the 100 day treatment of Ryan (2007).

Results

General

Frog tadpoles (*Hyla* sp., *Rana* sp.) were plentiful at the Hole and Kirtland's Pond throughout the study period, though there was a major reduction in the population density at Kirtland's Pond around the time the *A. texanum* larvae disappeared. The Hole was the only site to never experience filamentous algal growth and occasional blooms during the study period. Crayfish were found at all four sites and damselfly larvae were only found at the Hole and Kirtland's Pond. Dragonfly larvae were also found in Kirtland's Pond. Water beetles, water spiders, and caddisfly larvae were all seen at the Hole. A water mold (*Sapralignea*) also infected about half of the observed egg clutches at both the Maintenance and I-465 Ponds.

The Hole

Metamorphic individuals were attained only from the Hole. All other ponds dried out before metamorphic individuals could be captured. The initial bout of hatching for this site began just before 7 April and the first metamorphic individual was recorded on 4 June. Therefore the minimum time to metamorphosis for this site was approximately 2 months. This pond dried significantly between 7 June and the 30 June and dried up completely sometime between 15 July and 23 July, the last day that the sites were surveyed (Figure 2).

Kirtland's Pond

Hatching occurred at approximately the same time for this site as was seen at the Hole (7 April). Individuals disappeared between the 22 April and the 28 April collections. The tadpoles (*Hyla* sp., *Rana* sp.) which had been plentiful at this site were also greatly diminished in number at this time (Figure 3).

I-465 and Maintenance Ponds

The initial hatching event for the I-465 Pond took place between 22 April and 28 April. In the second collection week, however an individual was retrieved that was an order of magnitude heavier than any other in the sample. It was also about 5 stages of development ahead of the rest of the group as well. This individual was very similar in weight and stage of development to those individuals that represented the initial hatching bout for the Hole and Kirtland's Pond sites during that same week. This site dried up between 21 May and 26 May (Figure 4).

Hatching occurred at the Maintenance Pond at approximately the same time as the I-465 Pond group and dried up during the same time as well. No individuals were found at either site after this time (Figure 5).

Analysis

Of the four sites, two ponds dried before any individuals could metamorphose and the individuals from Kirtland's Pond disappeared three weeks into the study. Only individuals at the Hole were able to reach metamorphosis. The average mass and snout-vent lengths at metamorphs were 0.803 g (SD= 0.240 g) and 29.36 mm (SD= 2.63 mm)

respectively (Figures 6 and 7). Average daily growth rate varied considerably among the collection periods with no clear overall trend in growth rate over the study period (Figure 8). Minimum time to metamorphosis was determined to be approximately 2 months. The ponds retained water for approximately 33 days after hatching at both the I-465 and Maintenance Ponds and approximately 105 days after hatching for the Hole. Kirtland's Pond still retained water after the Hole had dried and the study period had ended. The percentage of metamorphic individuals at the Hole increased throughout the study period, sharply peaking the week before complete drying occurred (Figure 9). There seemed to be two distinct metamorphic pulses that came from the Hole (Figure 9). The average mass of metamorphs emerging from the Hole generally fell throughout the study period (Figure 10). A one sample t-test revealed that the metamorphs were significantly larger on average than those in the 100 d treatment of Ryan (2007) (t=3.48, df=20, t crit=2.09)

Discussion

The most probable explanation for the disappearance of the larvae at Kirtland's Pond is predation. Both caddisfly and dragonfly larvae, known predators of amphibian larvae (Rowe *et al.* 1994), were found at the site. Along with larval and aquatic insects, garter snakes (*Thamnophis* sp.) and water snakes (*Nerodia* sp.) are also common predators of larvae (Trauth, 2005) and may have possibly existed at this site, though they were never encountered during this study. In an experimental study done by Walston and Mullin (2007), the removal of predatory fish from ponds increased the larval period of *Ambystoma texanum* showing that predatory fish can have a significant impact on the survival and development rate of *A. texanum*. Since Kirtland's pond is a semipermanent

manmade pond, it is possible that there are predatory fish present in the pond that were not seen during the sampling bouts. All of these possibilities offer explanations as to the cause of the disappearance of these larvae from this site. It also exemplifies *A. texanum*'s poor adaptation for dealing with the challenges present in semipermanent and permanent wetland habitats.

The fate of the larvae at the Maintenance and I-465 pond sites reveal the harsh mortality rates that can occur when ephemeral ponds dry too early in the season. In 2009, the risk of desiccation outweighed the benefits of a predator free nuptial-natal site for these two locations. The unusually large individual found in the second week of sampling at the I-465 pond could indicate that there were a few individuals that had the potential to metamorphose in time, but this would require that there were other early hatching individuals who were even more developed than the individual that was found and that they were able to decrease their time to metamorphosis below the minimum time seen at the Hole site. Although these conjectures are unlikely, it does reveal that given another 2-3 week, metamorphic individuals could have escaped these sites. Also, these sites dried out early because there was no precipitation for a run of five days between the collection dates and this run was followed by a heavy rainstorm the day before the next collection date thereby refilling the ponds at both the sites. If this rainstorm had come a day or two earlier, the larvae at these sites could have continued to develop for many more weeks into the season, as the sites were checked for a few weeks following the loss of the larva population and over this time the wetlands were filled to some degree with water. From these two examples it is clear just how variable and unstable these habitats can be.

The Hole was the only site out of the four that produced metamorphic individuals before drying out in mid-July. In comparison to an experimental study done by Ryan (2007) that tested the effects of hydroperiod on *A. texanum*, my findings on the minimum hydroperiod needed to reach metamorphosis were found to be similar (approximately 2 months). These results are also consistent with past observations of a 2 month minimum hydroperiod (Minton 2001, Petranka 1998). A one-sample t-test also revealed that the metamorphs were significantly larger on average than those in the 100 d treatment of Ryan (2007) ($t=3.48$, $df=20$, $t\ crit=2.09$).

Ryan (2007) also made several other interesting findings about *A. texanum*. First, survival was unaffected by the hydroperiod treatments though hydroperiod did have an effect on completion of metamorphosis so in a real life situation, hydroperiod would have a dramatic effect on survival since all nonmetamorphosed individuals at the time of drying would die, as in the cases of the Maintenance and I-465 Ponds. Second, hydroperiod affected the time at metamorphosis, accelerating metamorphosis for shortening hydroperiods. There was no effect on size at metamorphosis though there was more variation in the longer hydroperiod and the control group than the intermediate hydroperiod group. Ryan suggested that a 2.5 month minimum hydroperiod was critical for a large portion of the larvae to reach metamorphosis.

There have been several other studies that have looked at the effects of hydroperiod on ambystomatid salamanders, including *A. texanum*. Phillips *et al.* (2002) found that time of hatching was a significant factor contributing to SVL at metamorphosis. Phillips found that SVL tends to decrease as individuals emerge later in the season. This was found to be significant for shorter hydroperiods, but not in longer

hydroperiods. Size at metamorphosis when compared to time of metamorphosis also decreases for short hydroperiods, though again there was no relationship seen in longer hydroperiods. These results parallel those found by Semlitsch *et al.* (1988).

It is interesting to compare *A. texanum* to other ambystomatid salamanders as life histories and intrafamily interactions can vary between species. For instance, Semlitsch *et al.* (1988) studied metamorphosis in *A. talpoideum*, a relative of *A. texanum*. This species, like *A. texanum*, is philopatric, metamorphoses in early to late summer (though may continue into fall), and the majority of individuals metamorphose within 2 months. Body size at metamorphosis did not differ for late versus early individuals nor did early versus late metamorphosis affect the age at first reproduction but, interestingly, those individuals who metamorphosed early were larger than the individuals who metamorphosed late at the time of first reproduction. Long hydroperiods seemed to lead to two distinct pulses of metamorphosis, similar to those seen at the Hole site, though individuals reached the same sizes at metamorphosis regardless of an individual's pulse group. Semlitsch noted some of the possible benefits of early metamorphosis as there being more time for terrestrial foraging during the early part of the season when resources are more plentiful thereby increasing their postmetamorphic body size. *A. talpoideum* was also able to delay metamorphosis until the pond begins to dry and is even known to become paedomorphic if the pond remains filled (Semlitsch 1987b).

Boone *et al.* (2002) also made interesting studies regarding interspecific interactions among ambystomatid salamander larvae. They found that timing of *A. opacum* hatching can change its interspecific relationship with *A. talpoideum* from *A.* competitive relationship to one of predation on the later hatching species. Boone also

noted some of the benefits of early hatching being more food, decreased vulnerability to aquatic insect predators, and decreased density of individuals at the time of emergence, though some of the benefits such as better foraging in terrestrial environments after early metamorphosis and extended foraging in the highly productive ephemeral pond as mentioned above (Semlitsch 1987b) are also possibilities as well. Early hatching can also be detrimental if rainfall is sporadic during the early part of the season and the pond dries in between these irregular events (Boone *et al.* 2002).

To bring it back to the species of interest in this study, there have been studies examining the plasticity for metamorphosis in *A. texanum* and the possible genetic link behind it. Petranka and Sih (1987) found that between two populations of *A. texanum* there existed a significant difference in the rate of metamorphosis. One population, which was later deemed to be representative of a distinct sister species, was found in an ephemeral stream while the other in a permanent pond. When Petranka and Sih conducted a common garden experiment they found that stream individuals still had shorter larval periods and emerged at smaller sizes at metamorphosis than pond individuals. Since they had been raised in the same environment, Petranka and Sih concluded that the dissimilarity in the rate of development between these two species was due to genetically based differences.

From the results of this study and many others, the importance of ephemeral ponds and hydroperiod in the life histories of many amphibian species, including *A. texanum*, is evident. They provide habitats with lower predation pressures and high primary productivity that the developing larvae can exploit before metamorphosing and entering the terrestrial environment and adulthood. We also see the risk taken by these

species by using these habitats, which often times results in mass mortality of larval populations. For these reasons it is imperative that current statutes be altered or new ones be put into place that provide for the protection of these types of wetlands. Temporary wetlands are considerably different from permanent ponds not only in the opportunities and costs that they offer but also in the species that they can support. Also, further research and field studies such as the one conducted here on *A. texanum* are necessary to gain a fuller picture of the life histories of this diverse group of animals. A richer understanding of the life histories of these families may be an important step in saving them from experiencing a mass extinction event within Class Amphibia.

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Figures

Figure 1. Range of *Ambystoma texanum* throughout the south central United States. Darker shading indicates regions with the greatest abundance.

Discover Life. *Ambystoma texanum: smallmouth salamander.* 2010. http://www.discoverlife.org/mp/20q?search=Ambystoma+texanum. Accessed: 2 April, 2010.

Figure 2. The frequency of individuals (y-axis) in each weight class (x-axis) for each given sample at the Hole site. Metamorphic individuals (stage 54 and above) are indicated with shaded bars. Graphs are standardized to a maximum frequency of 8. Bar breaks indicate frequencies exceeding the cut off and exact values for these bars are given above each broken bar. Letters represent sample dates as follows A: 4/14, B: 4/21, C: 4/28, D: 5/5, E: 5/12, F: 5/20, G: 5/26, H: 6/4, I: 6/11, J: 6/17, K: 6/24, L: 6/30, M: 7/7, N: 7/14. Missing letters indicate dates when no individuals were sampled from the site.

Figure 3. The frequency of individuals (y-axis) in each weight class (x-axis) for each given sample at Kirtland's Pond. Graphs are standardized to a maximum frequency of 8. Bar breaks indicate frequencies exceeding the cut off and exact values for these bars are given above each broken bar. Letters represent sample dates as seen in Figure 2.

Figure 4. The frequency of individuals (y-axis) in each weight class (x-axis) for each given sample at the I-465 site. Graphs are standardized to a maximum frequency of 8. Bar breaks indicate frequencies exceeding the cut off and exact values for these bars are given above each broken bar. Letters represent sample dates as seen in Figure 2.

Figure 5. The frequency of individuals (y-axis) in each weight class (x-axis) for each given sample at the Maintenance Pond site. Graphs are standardized to a maximum frequency of 8. Bar breaks indicate frequencies exceeding the cut off and exact values for these bars are given above each broken bar. Letters represent sample dates as seen in Figure 2.

Figure 6. Frequency of weights (g) of metamorphic individuals from the Hole.

Figure 7. Frequencies of snout-vent length (mm) of metamorphic individuals at the Hole.

Figure 8. The average daily growth rates for three of the four sites. Kirtland's Pond was excluded due to lack of consecutive data collection dates that could be used for analysis.

Figure 9. Percentage of metamorphic individuals per sample at the Hole site.

Figure 10. Average weight (g) for each site over the study period. Outlier individual from the Hole pulled from the average for that day and is represented by a separate point. The averages for metamorphic individuals at the Hole are also represented, though they were also included in the overall average for their respective collection days as well. Error bars were excluded to increase readability of the individual values in the figure.

Figure 1.

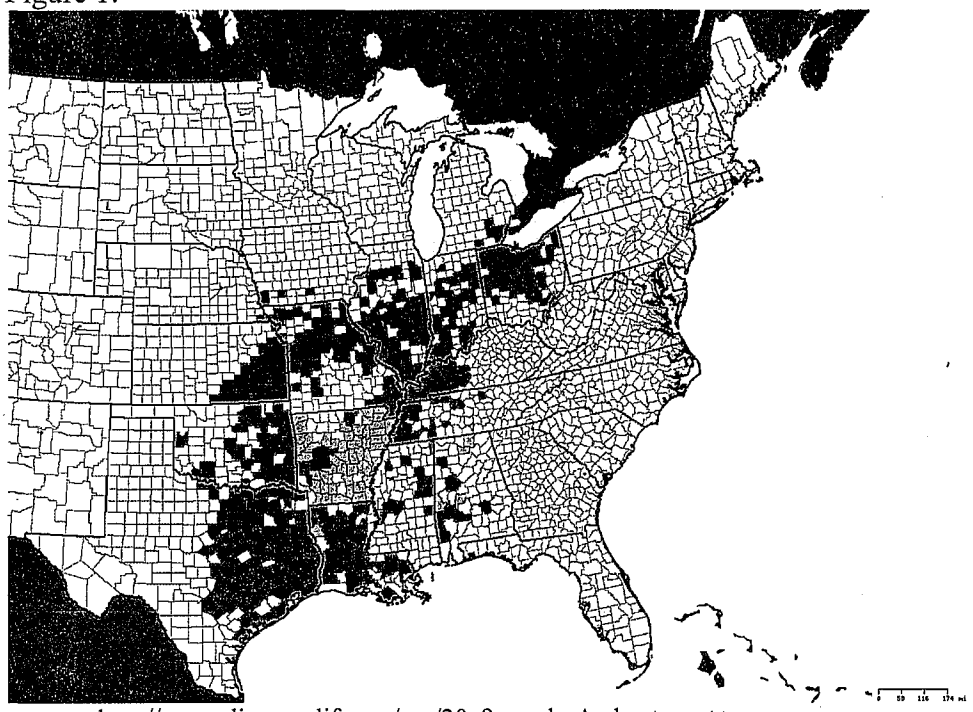

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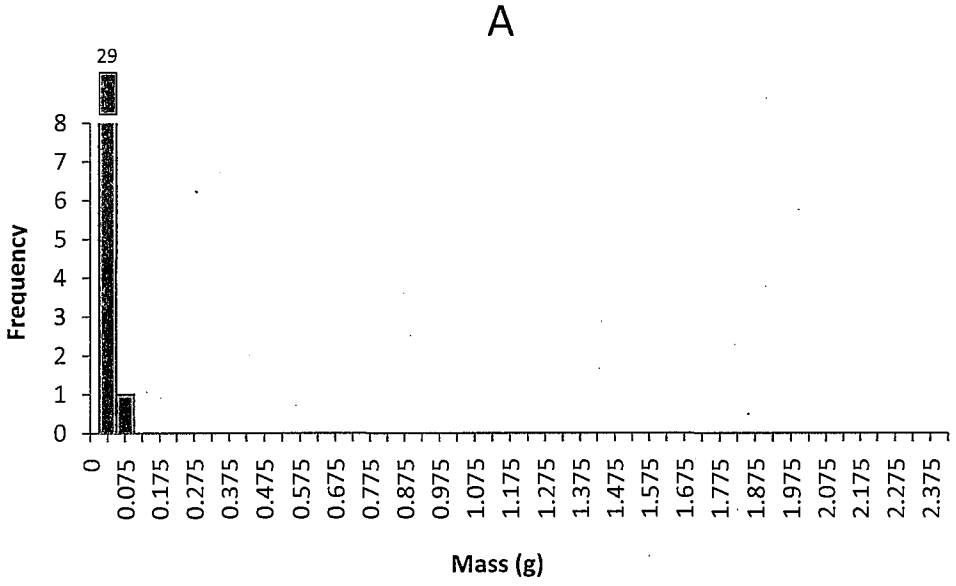
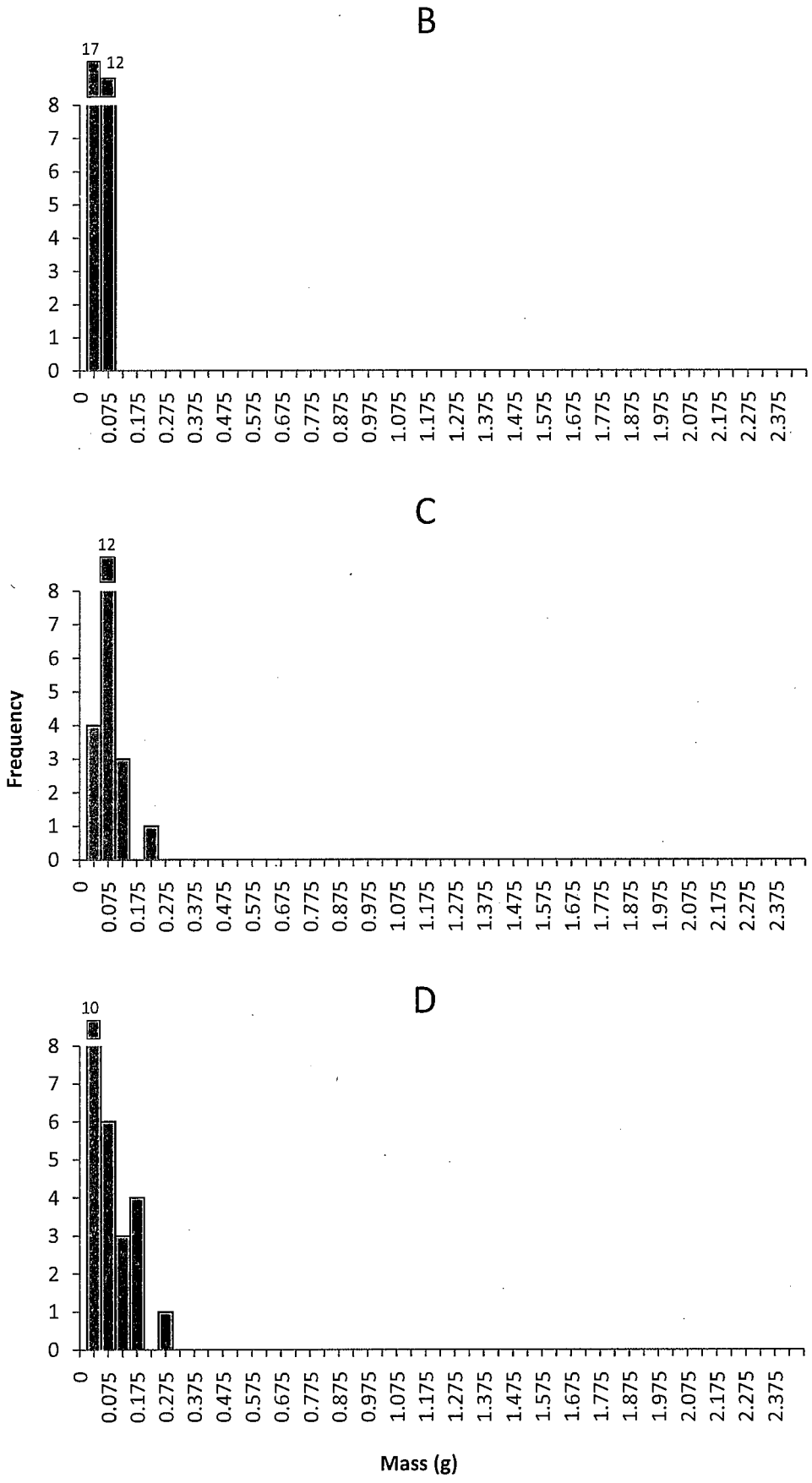
Figure 2

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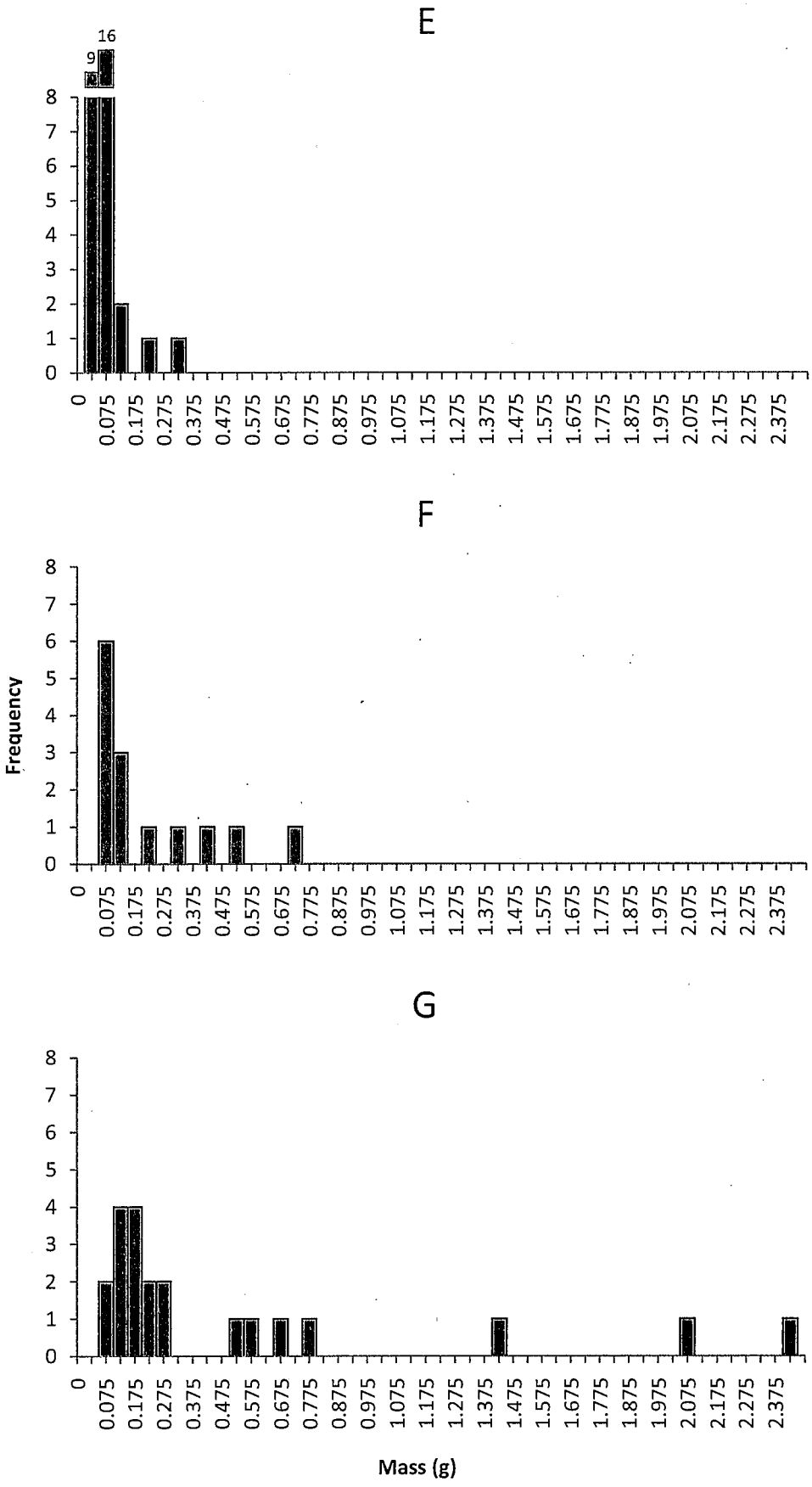
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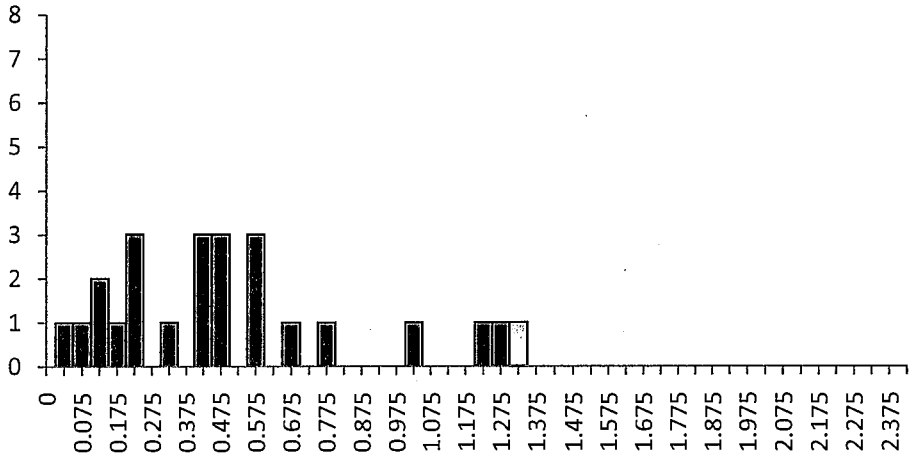
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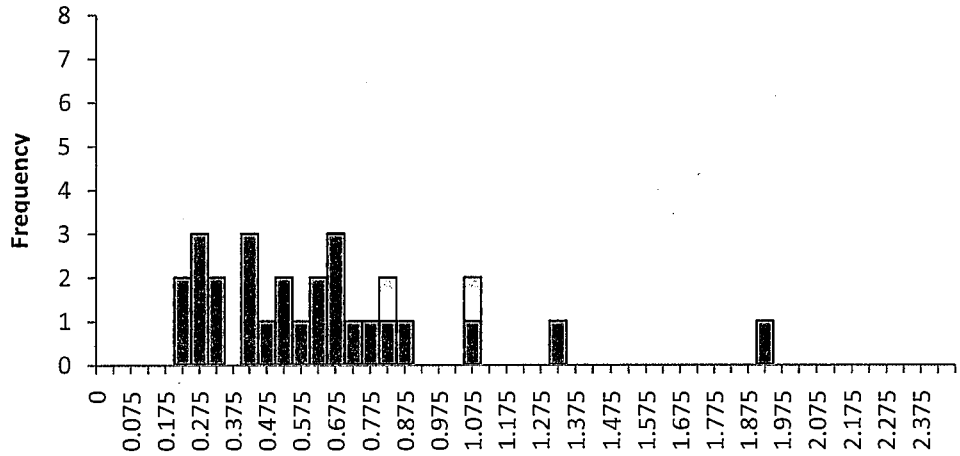
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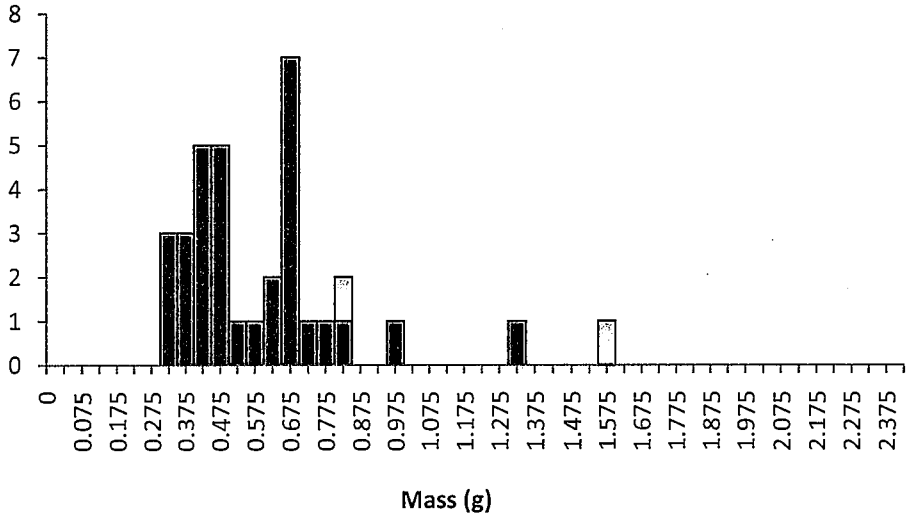
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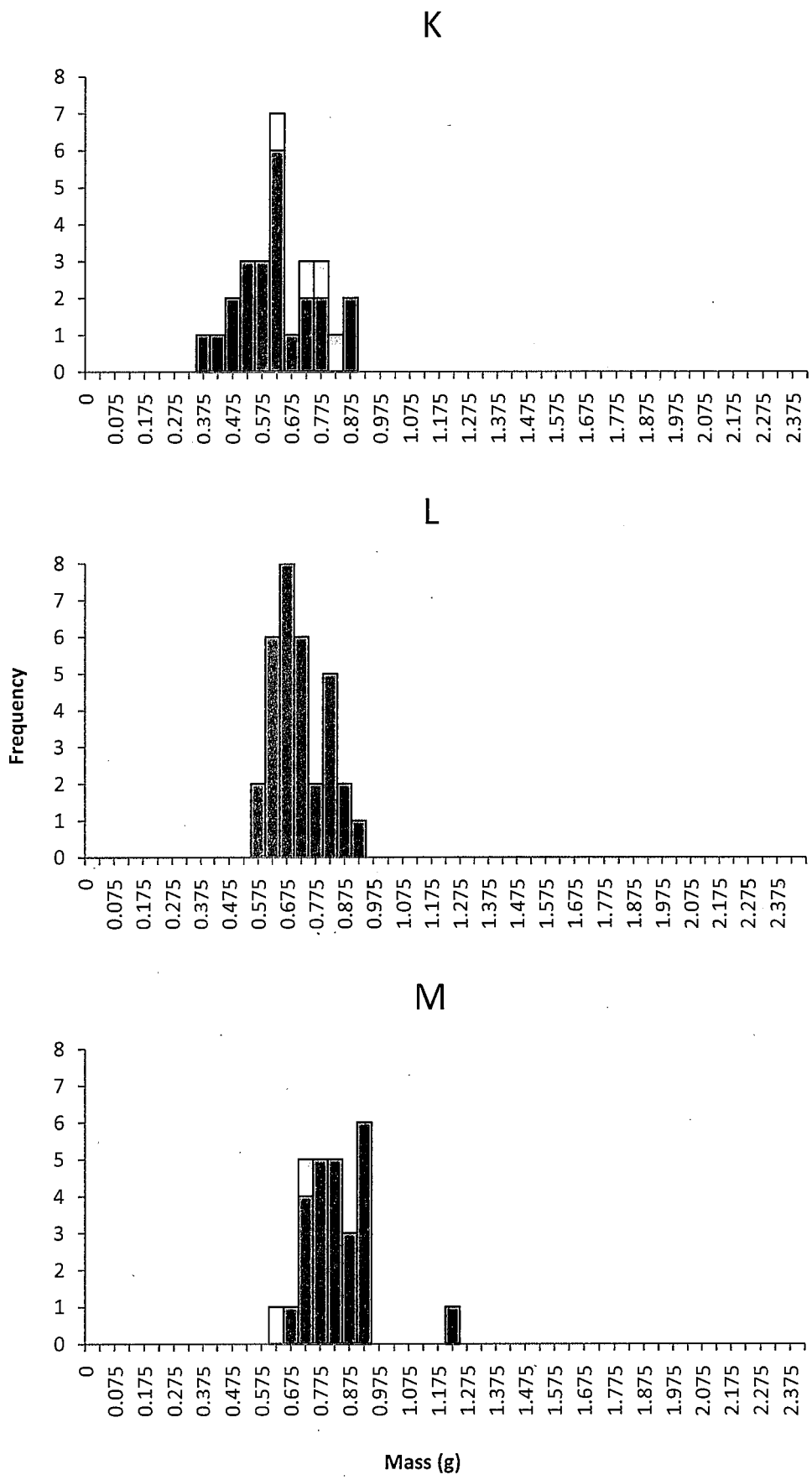
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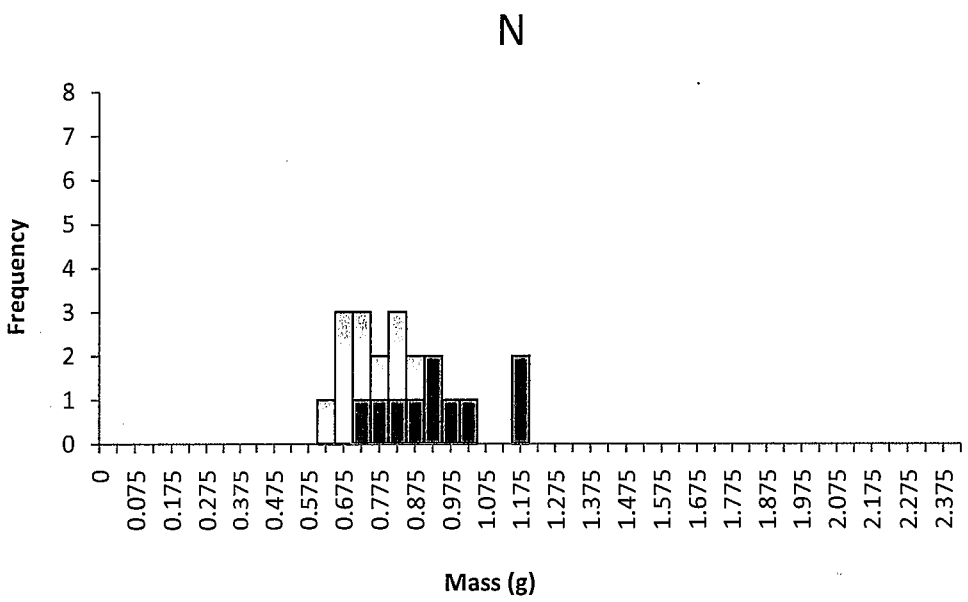
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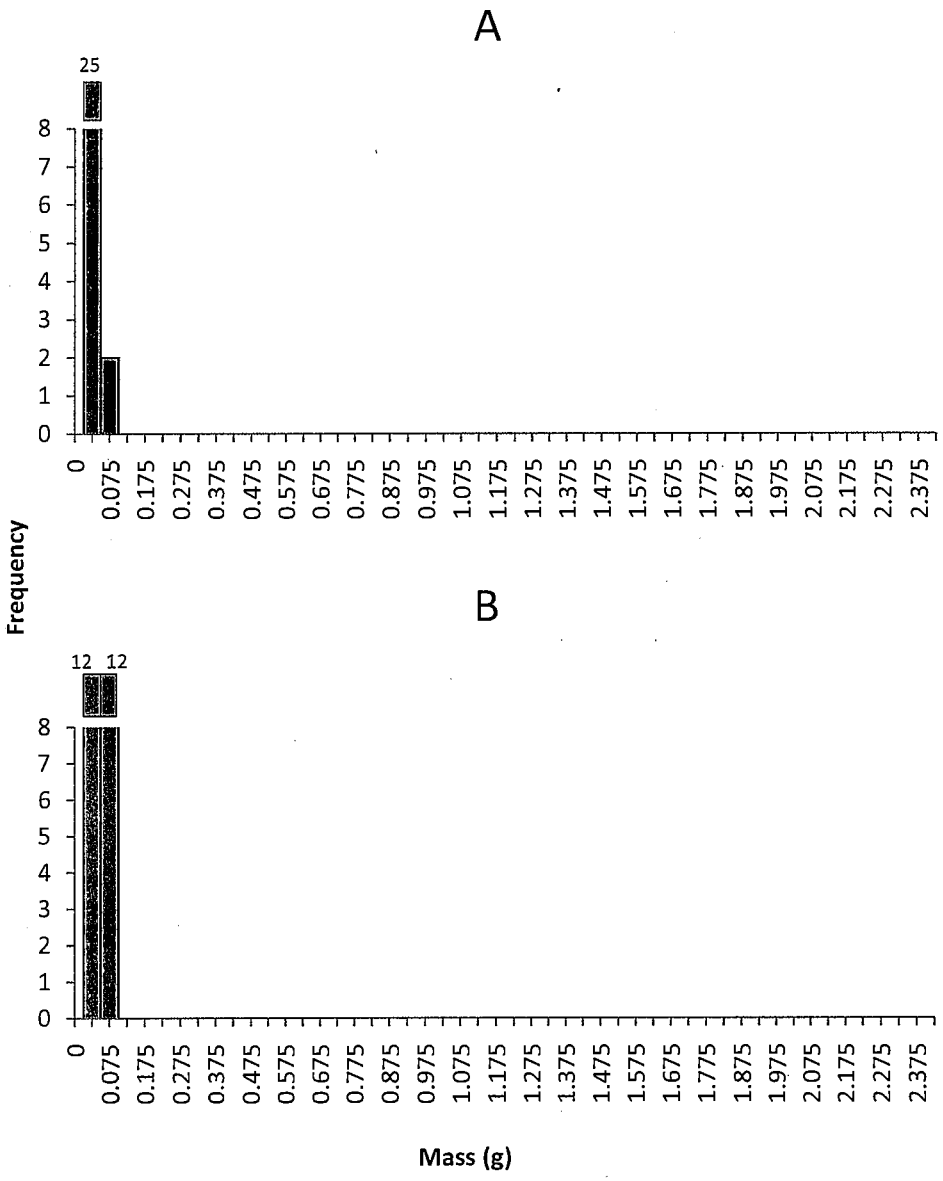
Figure 3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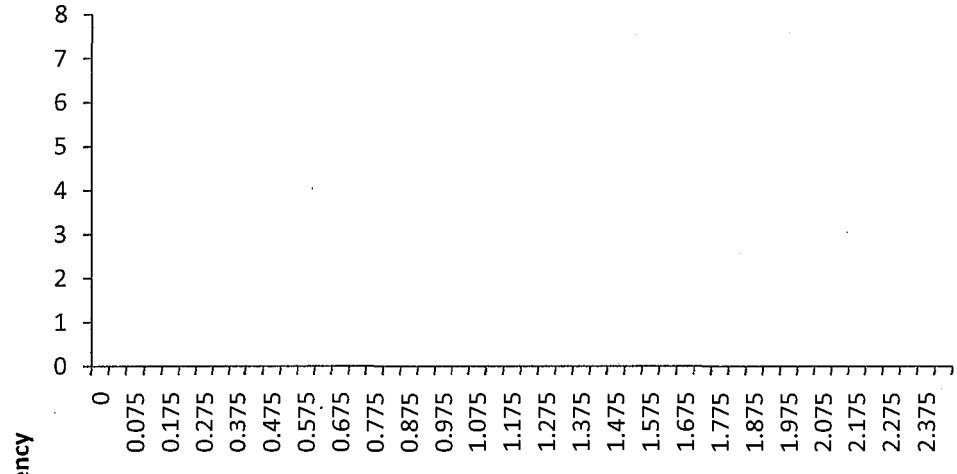
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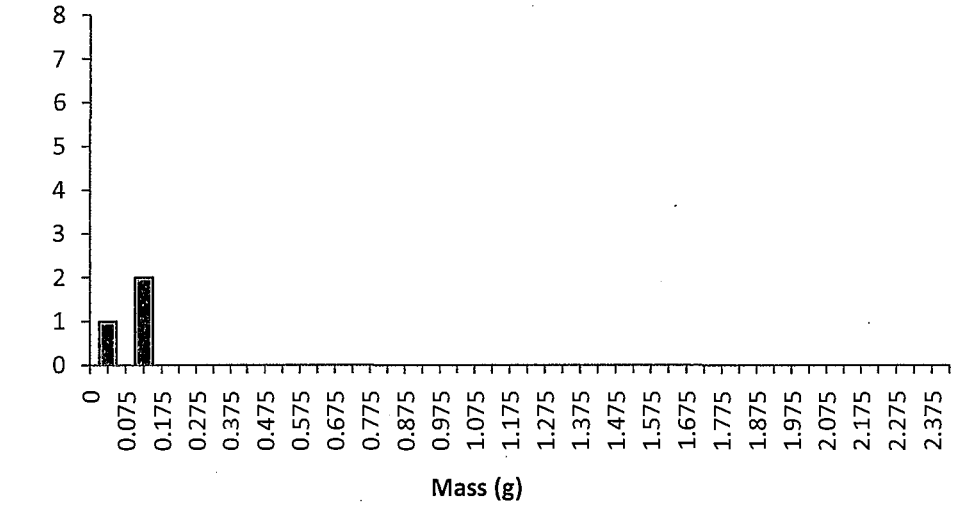
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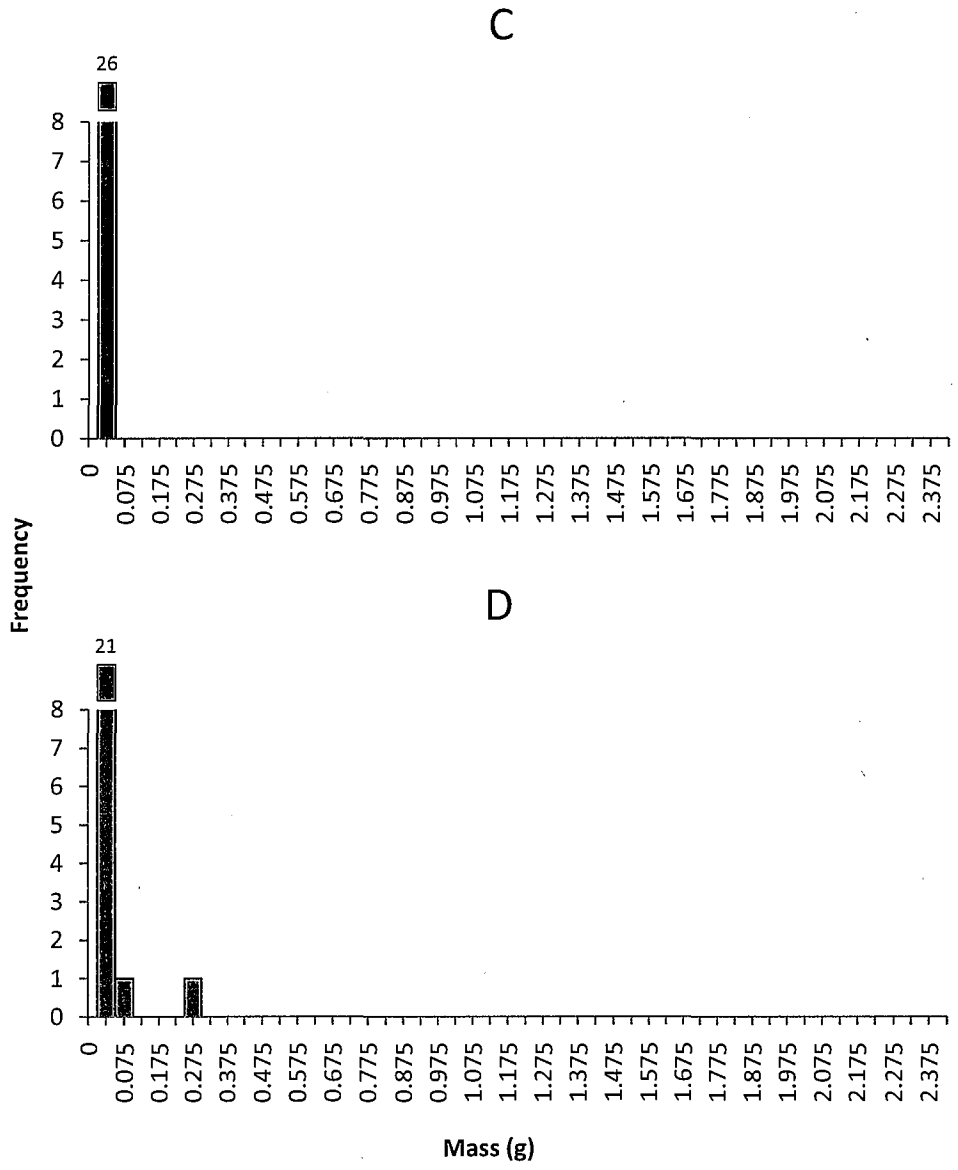
Figure 4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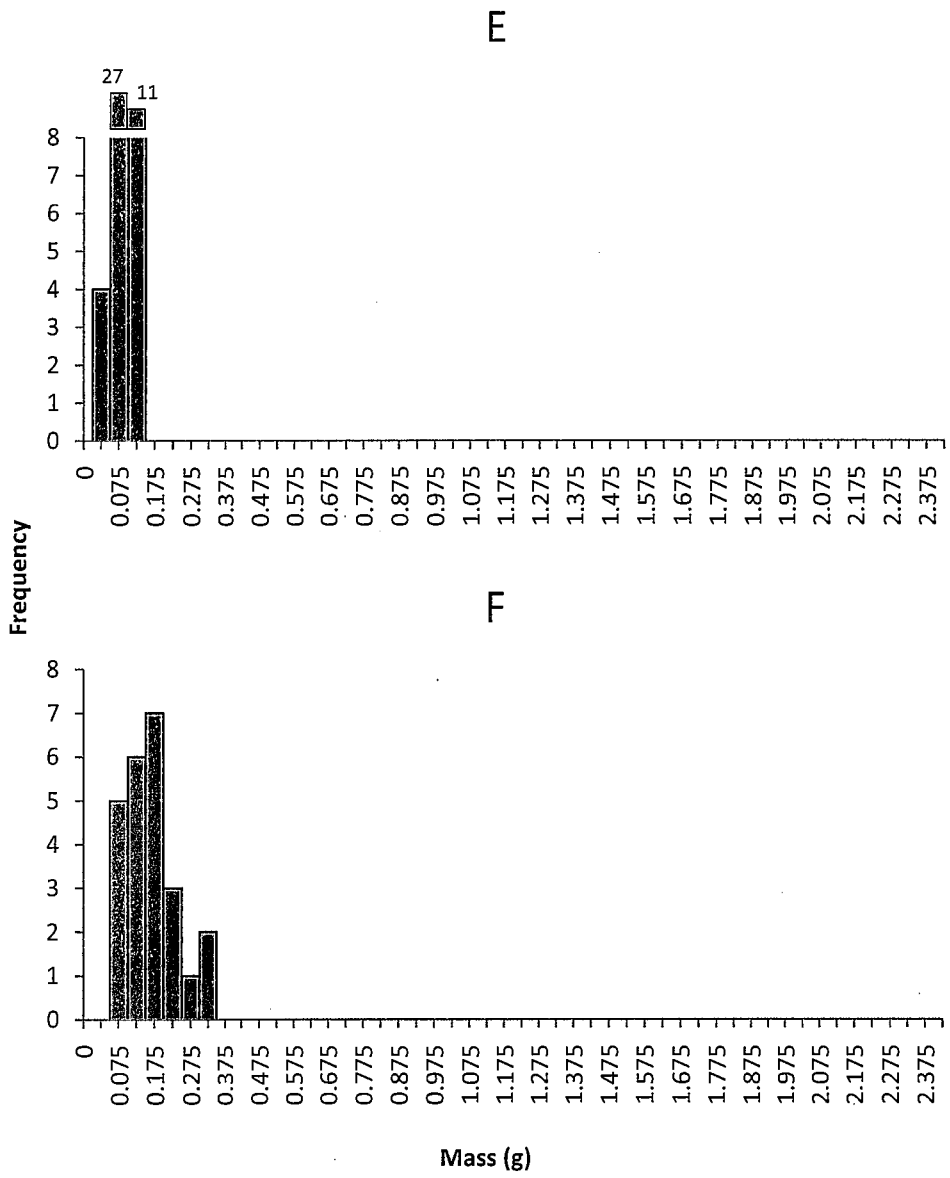
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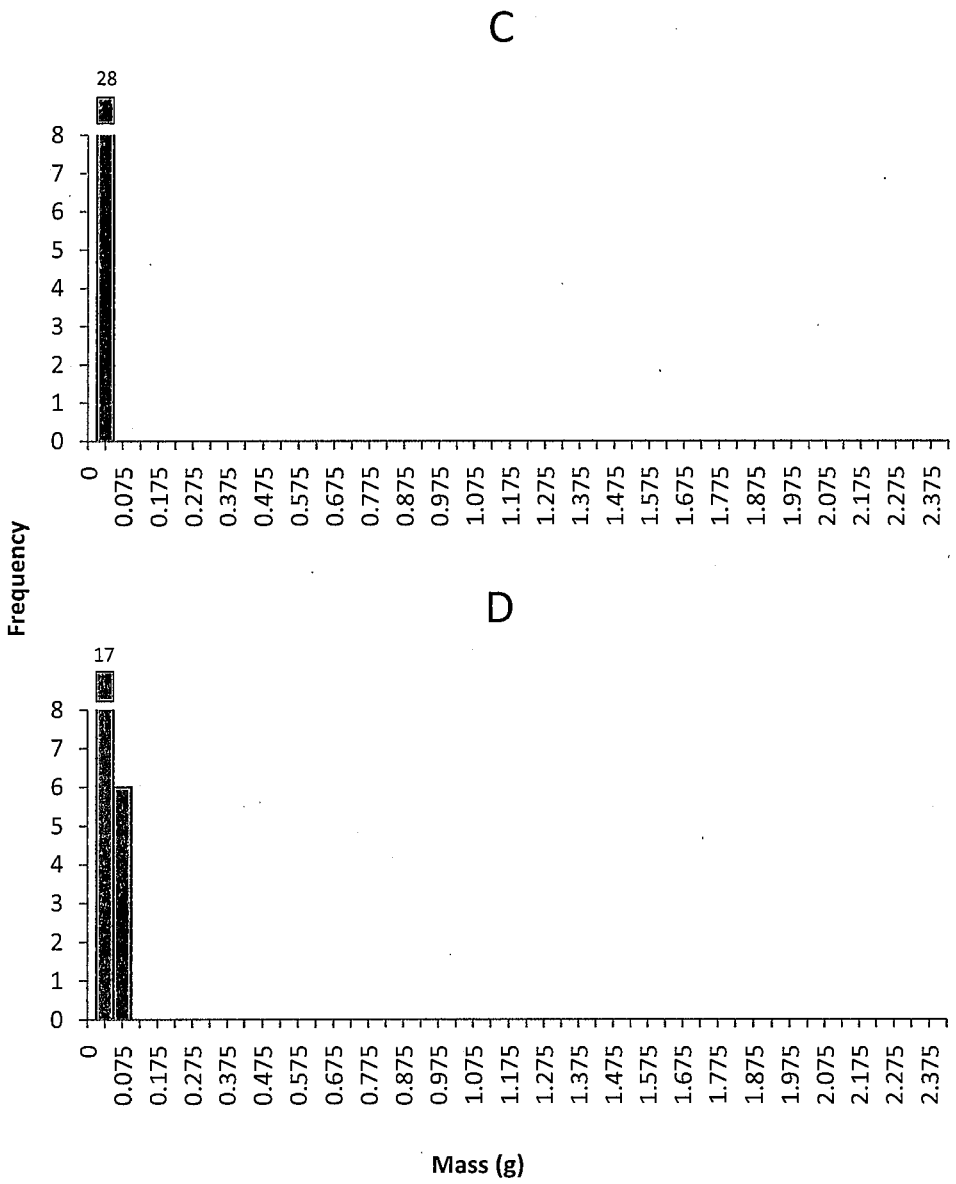
2.375

Figure 5


C
28
8
7
6
5
4
3
2
1
0
0
0.075
0.175
0.275
0.375
0.475
0.575
0.675
0.775
0.875
0.975
1.075
1.175
1.275
1.375
1.475
1.575
1.675
1.775
1.875
1.975
2.075
2.175
2.275
2.375
Frequency
D
17
Mass (g)

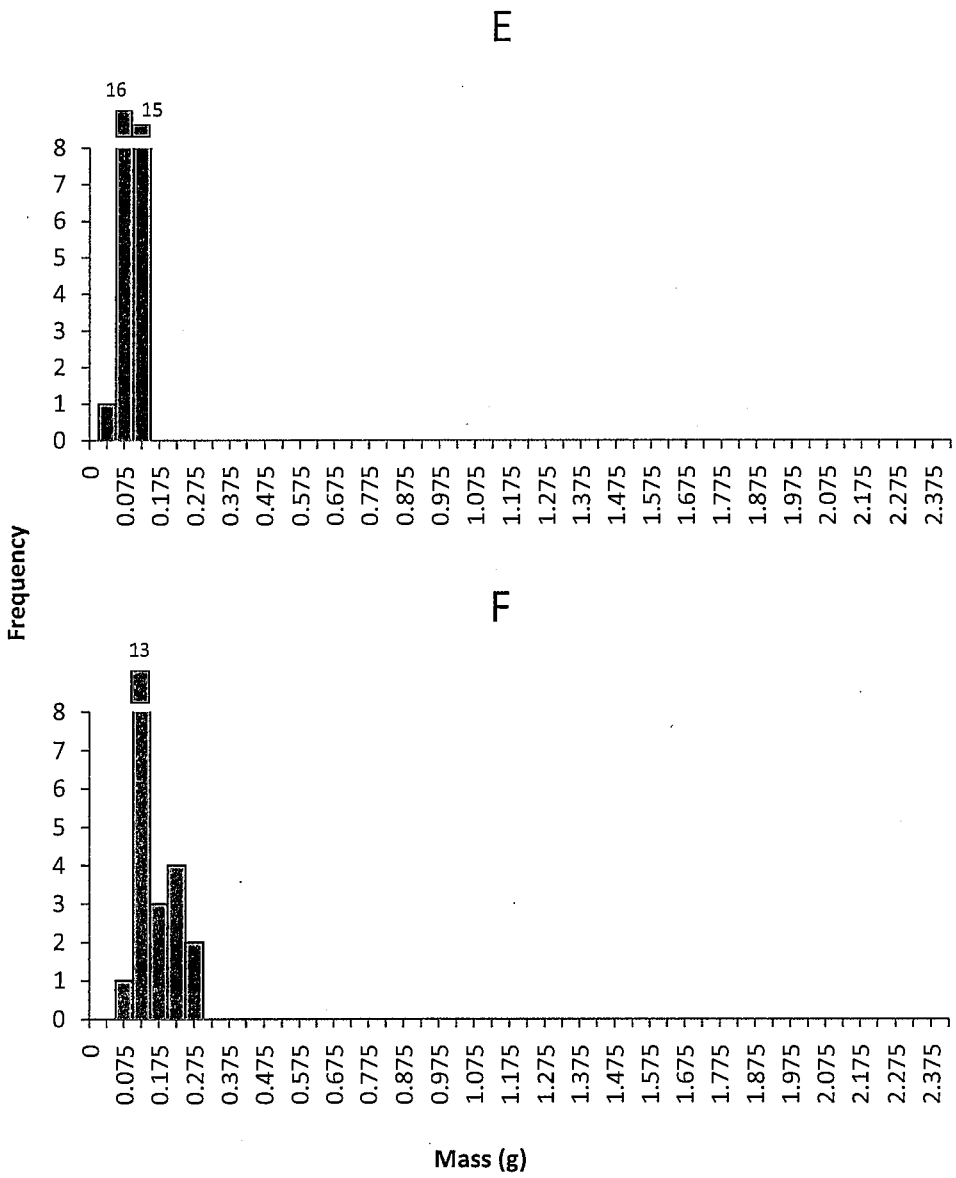

E
16
15
F
13
Frequency
Mass (g)
0
1
2
3
4
5
6
7
8
0
0.075
0.175
0.275
0.375
0.475
0.575
0.675
0.775
0.875
0.975
1.075
1.175
1.275
1.375
1.475
1.575
1.675
1.775
1.875
1.975
2.075
2.175
2.275
2.375

Figure 6

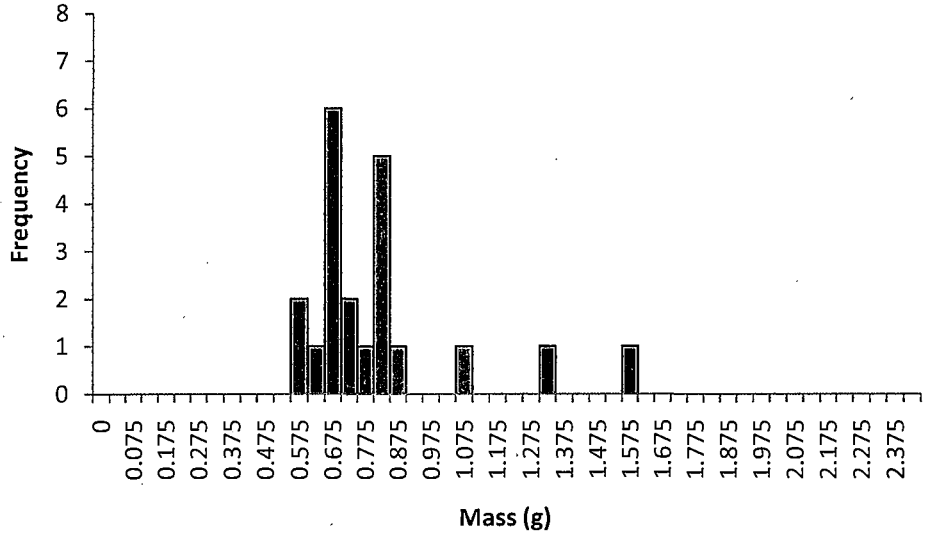


Figure 7

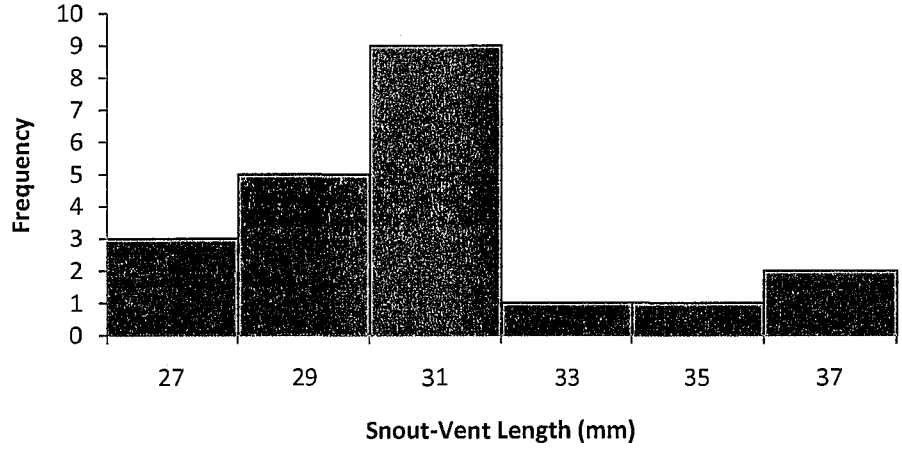


Figure 8

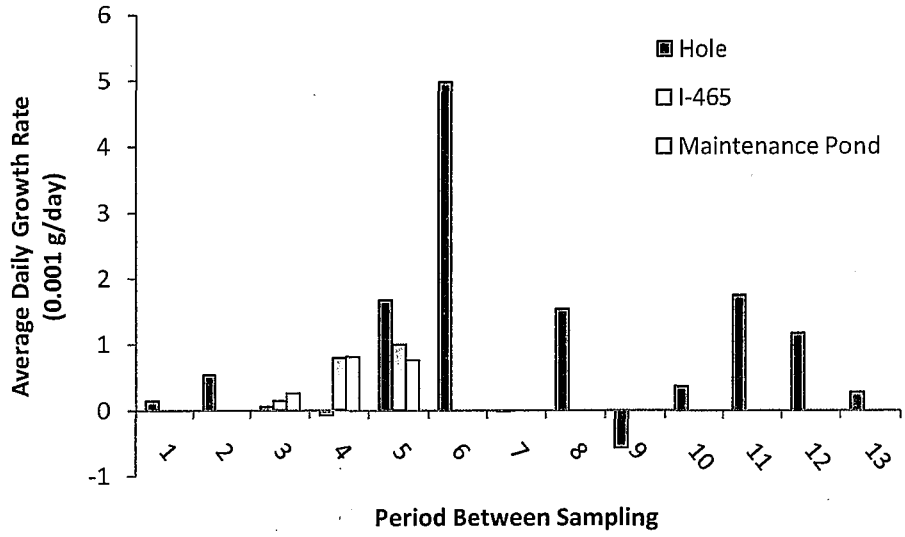


Figure 9

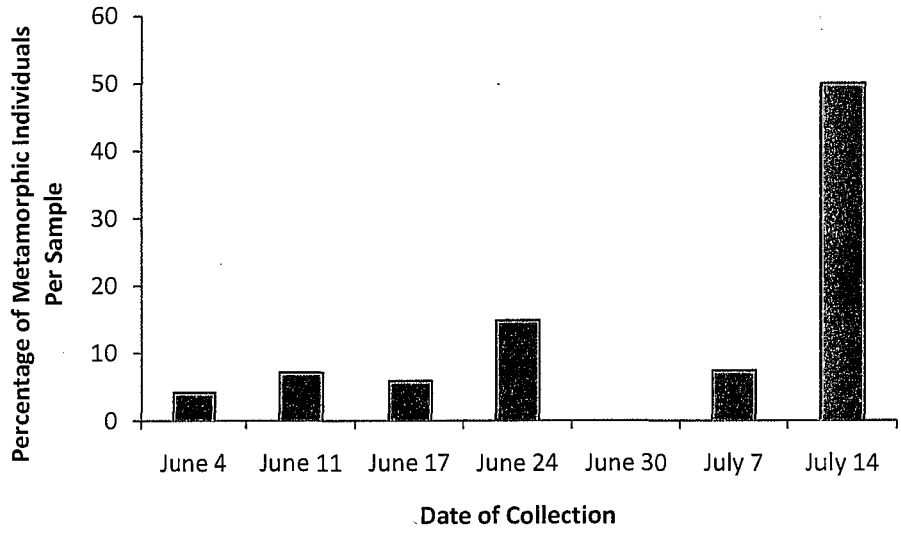
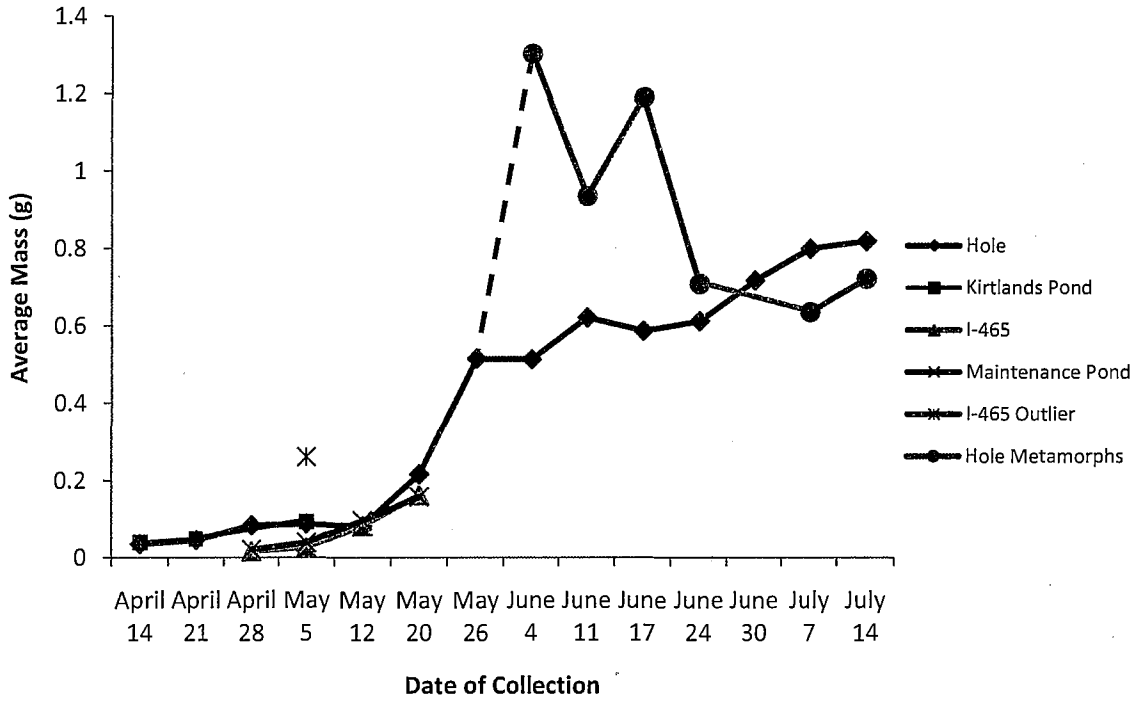


Figure 10


1.4
1.2
1
0.8
0.6
0.4
0.2
0
Average Mass (g)
April 14
April 21
April 28
May 5
May 12
May 20
May 26
June 4
June 11
June 17
June 24
June 30
July 7
July 14
Date of Collection
Hole
Kirtlands Pond
I-465
Maintenance Pond
I-465 Outlier
Hole Metamorphs